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Citation for published version:

Cohen, MH & Ackland, GJ 2012, 'Boundaries between Ancient Cultures: Origins and persistence', *Advances in Complex Systems*, vol. 15, no. 1-2, 1150004. <https://doi.org/10.1142/S0219525911003220>

Digital Object Identifier (DOI):

[10.1142/S0219525911003220](https://doi.org/10.1142/S0219525911003220)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Advances in Complex Systems

Publisher Rights Statement:

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BOUNDARIES BETWEEN ANCIENT CULTURES: ORIGINS AND PERSISTENCE

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Received 16 December 2010

Revised 5 May 2011

Published 6 January 2012

In a recent work on the wave of advance of a beneficial technology and associated hitchhiking of cultural and biological traits, we simulated the advance of neolithic agriculture into Europe. That model embraced geographical variation of land fertility and human mobility, conversion of indigenous mesolithic hunter-gatherers to agriculture, and competition between invading farmers and indigenous converts. A key result is a sharp cultural boundary across which the agriculturalists' heritage changes from that of the invading population to that of the converts. Here we present an analytical study of the cultural boundary for some simple cases. We show that the width of the boundary is determined by human mobility and the strength of competition. Simulations for the full model give essentially the same result. The finite width facilitates irreversible gene flow between the populations, so over time genetic differences appear as gradients while e.g. linguistic barriers may remain sharp. We also examine the various assumptions of the model relating to purposeful versus. random movement of peoples and the competition between cultures, demonstrating its richness and flexibility.

Keywords: Wave of advanced; Neolithic; culture; boundary; Neanderthal; agriculture; Indo-European; computer model.

1. Introduction

Mathematics has become established as the language of science, but its usefulness deteriorates as the complexity of the system under study increases. Thus while quantum physics produces extremely accurate predictions, chemistry is in less exact correspondance and mathematical biology still poorer. One can debate how useful such techniques are in examining human prehistory.

From an archaeological perspective, it is worth recapping what modeling and simulation can and cannot hope to achieve. Firstly, we distinguish between modeling, mathematics and simulation. A *model* is based on experience and data, although it is not a fit to data: it is an explanation of the key factors which underlie the history. *Mathematics* allows us to define rigorously a verbal argument from which formal proofs of the logical consequences of the argument can be made. A *simulation* is a solution to the model in a complex situation, with parameters fitted to data, which can expose how the model would play out in the real world. Mathematics and simulation bring no opinions or value judgements, they are merely a way of showing what the consequences of the model are, such that the model can be evaluated against the archaeological record.

However, their key advantage is that the argument from premise to conclusions is rigorous. Thus rival premises can be examined and discrepancies between model conclusions and observations can be clearly traced to erroneous premises. This is most useful if the model is a “null hypothesis”, incorporating the fewest assumptions to see if they are sufficient to explain the observations.

Here we discuss the features which should be considered in building a mathematical model of the emergence and spread of human populations. We are strongly influenced by the arguments and models of Ammermann and Cavalli-Sforza, Fort and Renfrew [3, 4, 19–21] which we extend to multiple populations. Previously, we showed how the parameters of this “wave of advance” model can be related to biogeographical data and presented simulations for Europe, India and Africa [1]. We present some mathematical results to show how distinct cultural boundaries arise in the model and to determine their stability.

2. Mathematical Models of the Wave of Advance

Underlying our model is the obvious premise that food is essential to animal life. For most of the existence of humans and of our ancestral species, food was procured by scavenging or hunting and/or gathering, methods attaining a high level of sophistication by the mesolithic. With the introduction of neolithic agriculture, food procurement was enriched by active production, a profound technological transformation. Agriculture was independently invented in 8–10 places around the globe from each of which it spread outward, generating major increases in population density. The manner of its spreading has long been debated: was it carried by an advance of the population of those who invented it — a *demic flow* [24, 25], was it adopted by the indigenous people, mesolithic hunter–gatherer societies — a process of *technology diffusion* [16, 22], or was it a combination of both with intermarriage, varying from case to case.

There are three sources of information to draw upon in formulating answers to these questions: archaeology, linguistics and genetics. However, ambiguities abound in the interpretation of the data each provides in the context of the advance of agriculture. Model-based quantitative analysis in the form of analytic theory, numerical

simulation, or some combination of both can assist in distinguishing among existing interpretations and suggesting new possibilities.

Models of the spread of agriculture have now evolved through three generations. The first generation consists of the wave of advance model of Ammermann and Cavalli-Sforza [3, 4]. They noted that the archaeologically established dates of local initiation of agriculture in Europe could be interpreted as a wave of advance propagating out of the fertile crescent at a speed of 1 km/year. They modeled the wave of advance as a solution of the FKPP equation,

$$\frac{\partial n}{\partial t} = D\nabla^2 n + \frac{1}{\tau}n(1 - n), \quad (1)$$

introduced by Fisher [11] and Kolmogorov *et al.* [18] to describe the advance over space and time of an advantageous gene into a population. It is well-known that this model supports a single wavefront advancing with velocity $c = 2\sqrt{D/\tau}$. The two parameters are D , the “diffusion constant” and τ , the time taken for a small population to increase 2.7-fold. AC took τ to be one generation and back-deduced a value for D from the observed wave-speed, reassuringly finding that it corresponded to an anthropologically reasonable value. Here, in the context of the advance of neolithic agriculture,

$$n = N/N_s \quad (2)$$

is the ratio of the local population density $N(\mathbf{r}, t)$ to the maximal (saturation) population density $N_s(\mathbf{r})$ which could be supported at that position, $0 \leq n \leq 1$.

Later, a time-delayed version of the FKPP equation, effectively considering only women of childbearing age has been studied [12, 13], while further work addressed the consequences of the discreteness of population and has introduced more detailed descriptions of the demic flow within the AC model [14, 15]. This significantly clarified the relationship between model parameters and anthropological records.

In forming a second generation model (C), Cohen [8] addressed the modification of the AC model necessary to account for variation of the fertility of the land for neolithic farming, in addition rederiving a Fisher-type equation from detailed consideration of the dependence of birth and death rates on food production and population density. The resulting equation,

$$\frac{\partial n}{\partial t} = \frac{1}{N_s} \nabla \cdot (DN_s \nabla n) + \frac{1}{\tau} \frac{n_1 + n}{n_0 + n} n(1 - n) \quad (3)$$

guarantees that no net demic flow occurs when the carrying capacity of the land is reached despite the locale dependence of $N_s(\mathbf{r})$. The factor $\frac{n_1 + n}{n_0 + n}$ in the logistic term in Eq. (3) takes into account the effects of population density and fertility dependence of food production rates on birth and death rates. The parameters N_s, n_0, n_1 and τ depend in turn on more fundamental parameters relating primarily to culture, human biology, and land fertility. This model supports a wave of advance with a speed of

$$c = 2\sqrt{(n_1/n_0)(D/\tau)}. \quad (4)$$

Subsistence boundaries exist beyond which the growth rate $1/\tau$ and N_s vanish. The wave of advance stops at subsistence boundaries because $1/\tau$ vanishes there.

Renfrew examined the implications of the AC wave of advance model for the spread of languages. In particular, he proposed that the wave of advance of agriculture into Europe carried with it the Indo-European languages, while into India it carried Dravidic, with Indo-European following on a later expansion.

The third generation model (ASSC) [1] involves combining the spatial dependence of the fertility with the idea of three discrete populations: original farmers (F), indigenous hunter-gatherers (H), and converts (X) who adopt the farming technology without adopting some marker cultural trait or traits of the original farmers and conversion from one population to another [5]. It addresses this issue of hitchhiking of cultural traits alongside advantageous technology. Terms representing the kinetics of conversion to farming, the competition for land use, and inter-cultural assimilation were incorporated into the model, resulting in the following equations:

$$\begin{aligned} \frac{\partial n_F}{\partial t} = & \frac{1}{N_s^F} \nabla \cdot (DN_s^F \nabla n_F) + \lambda n_F n_X (n_F - n_X) \\ & + \frac{1}{\tau_F(N^t)} n_F (1 - n_F - n_{FH} - n_{FX}), \end{aligned} \quad (5a)$$

$$\begin{aligned} \frac{\partial n_H}{\partial t} = & \frac{1}{N_s^H} \nabla \cdot (DN_s^H \nabla n_H) - \gamma_H n_H (n_F + n_X) \\ & + \frac{1}{\tau_H(N^t)} n_H (1 - n_H - n_{HF} - n_{HX}), \end{aligned} \quad (5b)$$

$$\begin{aligned} \frac{\partial n_X}{\partial t} = & \frac{1}{N_s^X} \nabla \cdot (DN_s^X \nabla n_X) + \gamma_X n_H (n_F + n_X) - \lambda n_F n_X (n_F - n_X) \\ & + \frac{1}{\tau_X(N^t)} n_X (1 - n_X - n_{XF} - n_{XH}). \end{aligned} \quad (5c)$$

Here D is the demic diffusivity, assumed the same for all three populations. $\tau_i(N^t)$ sets the timescale for the increase of each population $i = F, H, X$. $N^t = \sum_i N_i$ is the total population density of all types, which enters τ_i in a way similar to $1/\tau \frac{n_1+n}{n_0+n}$ in [8, Eq. (3)]. $N_s^i(\mathbf{r})$, the maximum population possible (“saturation”). The n_i are the fractions of its maximum population currently attained by population, i and $n_{ij} = n_j N_s^j / N_s^i$ means that competition enters in a way derived from the assumption that each extra person in a region can occupy (or defend) an equal amount of land regardless of whether that extra person is F, H or X. This reduces the land available for others to grow food. The parameter γ_H sets the timescale for conversion of H to X with $\gamma_X = \gamma_H N_s^H / N_s^X$. λ sets the rate at which X are assimilated into the F culture and vice versa. It is thus assumed that nobody dies in conversion or assimilation.

Although their derivation is lengthy, Eqs. (5) alone constitute the ASSC model. It was parameterised for simulation of the advance of Neolithic agriculture into

Europe and India and of the much later advance of European agriculturalists into southern Africa. Time-dependence of coastlines, variable geographic fertility and the terrain-dependence of D were all included using available data. Several findings are worthy of particular note. First, a *moving cultural boundary* between F or X and H is formed — equivalent to the AC wave of advance. Second, a *cultural boundary* can form between F and X, behind which F, and ahead of which X, live at saturation densities. This boundary forms on a timescale $1/\gamma_H$ and has width $\sqrt{D/\lambda}$: it moves slowly and ultimately follows lines of low fertility. Third, *subsistence boundaries* can form, with geography causing the FH wave to be diffracted at bottlenecks such as around the Bosphorus, Black Sea and Northern Italy, which can give rise to distinctive cultures.

For the specific parameterisations in Ackland, *et al.* (2007), the cultural boundary was found within Europe running southwest to northeast, Fig. 1. In India the cultural boundary runs into the Himalayas, splitting the X population in a way comparable to the geographical bifurcation of the Dravidian languages.

Compared with the archaeological evidence, the model fails to show the wave front sufficiently elongated along the Rhine-Danube or Indus corridors. It also fails to produce island and early coastal development. This failure of the model as null hypothesis is clear evidence for the importance of waterways [9].

These findings are important and controversial enough to warrant deeper mathematical and structural analysis of the model. The discovery of the cultural boundary has important implications for genetic gradients and trees, and for language trees as well. According to the model, demic flow occurs across the cultural boundaries and is balanced by cultural assimilation within the majority population, thus providing a continual flow of genetic material, which assimilation cannot destroy.

Accordingly, in the present paper we carry out an analytic study of the persistence of a stationary cultural boundary within a *homogeneous* terrain (i.e. N_s^i constant). We shall show the FX boundary to be marginally stable in infinite, homogeneous terrain, destabilized by coastlines and regions of increased fertility, but stabilised by regions of decreased fertility into which the boundary can lock.

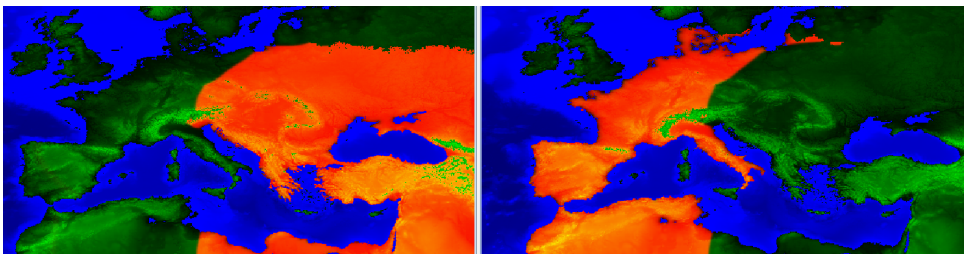


Fig. 1. (Color online) A cultural boundary formed in simulations with the full model based on a fertility map of Europe. The left panel shows the final distribution of invading neolithic farmers; the right panel shows the area occupied by converts to farming technology. Orange shows the population density, while shades of green indicate the fertility $N_s^i(\mathbf{r})$.

We shall first illustrate the richness and flexibility of the ASSC model by discussing the advance of a single population into virgin territory, the emergence of an advantageous technology (farming), and the advance either by demic flow or by technology diffusion of the advantageous technology as a moving cultural boundary. The next sections are primarily mathematical, but we summarize the archaeological meaning of the results at the end.

3. Wave of Advance as an Advancing Cultural Boundary: Mathematical Analysis

The populations at any point in space x and time t can be labelled by $n(x, t) = (n_F(x, t), n_H(x, t), n_X(x, t))$. In this notation, the ASSC model allows five spatially uniform fixed points, as follows:

$(0, 0, 0)$ is trivial — no people, and is unstable to any fluctuation.

$(0, 1, 0)$ hunters everywhere is the typical starting configuration: it is unstable to fluctuations in n_F or n_X . It is this instability that gives rise to the wave of advance F or X into a saturated population of H.

$(0.5 \ 0 \ 0.5)$ is unstable against a general fluctuation in n_F and/or n_X . This would be the population composition locally at a stationary cultural boundary between F and X such as we had observed, e.g. in our simulation of the advance of farming into Europe, Fig. 1, and its instability raises questions about the persistence of stationary cultural boundaries in homogeneous terrains which we address in the next section.

$(1, 0, 0)$ and $(0, 0, 1)$ are the only globally uniform stable states. A persistent cultural boundary manifests as a stable inhomogeneous population between the corresponding two locally uniform and locally stable states. As we shall see in Sec. 4, a suitable local inhomogeneity in fertility is required for its existence.

In the absence of such an inhomogeneity, the advantageous technology advances, borne either by its originator farming population (F) or converts (X). There is a moving cultural boundary between peoples having and not having the technology, the wavefront of the wave of advance. In our model, this cultural boundary is between non-equivalent populations, and one can expect to find cultural artifacts representing each group.

3.1. *Emergence of hunters/gatherers from ice age refugia*

At the end of the last ice age, Mesolithic hunter/gatherers were localized in refugia, for example in Europe in the Spanish/French, Moldavian, and Ukrainian refugia. As the climate warmed, they expanded outward into Europe in waves of advance resulting in saturation of all suitable landscapes. the emergence of each wave was probably constrained by environmental evolution rather than governed by the population dynamics modeled by the FPKK equation. Nevertheless, in this section we shall use the FPKK equation as a way to introduce the mathematical methods we

shall use to analyze applications of the more complex ASSC model. We consider a single population of hunters H of density N in its early stage of emergence from a refugium into a one-dimensional terrain. The population density is then well below saturation, $N \ll N_s$, where N_s is the saturation population, so that the FPKK can be linearized

$$\frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} + \frac{1}{\tau} N. \quad (6)$$

In later applications, we find that the ASSC equation can be linearized and separated to adopt the same form.

We solve this equation using a Fourier Transform method.

To solve this, let the initial condition be $N(x, 0)$ and define a Fourier transform over space,

$$M(k, t) = \int e^{-ikx} N(x, t) dx,$$

$$N(x, t) = \frac{1}{2\pi} \int e^{ikx} M(k, t) dk,$$

$$M(k, 0) = \int e^{-ikx} N(x, 0) dx,$$

$$N(x, 0) = \frac{1}{2\pi} \int e^{ikx} M(k, 0) dk.$$

Inserting $N(x, t)$ into (6) and using Fourier transform,

$$\frac{dM(k, t)}{dt} = \left(-Dk^2 + \frac{1}{\tau} \right) M(k, t), \quad (7)$$

which implies

$$M(k, t) = M(k, 0) \exp \left(-Dk^2 + \frac{1}{\tau} \right) t. \quad (8)$$

For the initial condition $f(x)$ on the population $N(x, t)$ of the refugium, we assume a Gaussian (normal) distribution for a total of ν hunters who are initially localized in a region of width σ around $x = 0$,

$$f(x) \equiv N(x, 0) = \nu \frac{\exp(-x^2/2\sigma^2)}{\sqrt{2\pi\sigma^2}}, \quad (9)$$

from which it follows immediately that $M(k, 0) = \nu \exp(-\sigma^2 k^2/2)$, and therefore: $M(k, t) = \nu \exp[-(Dt + \sigma^2/2)k^2 + t/\tau]$, which can be inverse transformed to give the time and position dependence of the population:

$$N(x, t) = \frac{\nu}{\sqrt{\pi(4Dt + 2\sigma^2)}} \exp[-x^2/(4Dt + 2\sigma^2) + t/\tau]. \quad (10)$$

Given this exact solution, we need to know whether it will develop into a wavelike form. A characteristic of a wave-like solution is that the point (x_A) where the

number density has fixed value A moves at constant speed $v = |dx_A/dt|$ independent of time and the value of A

Substituting $x = x_A$ and $N(x, t) = A$, and solving for x_A gives

$$x_A = \pm \sqrt{(4Dt + 2\sigma^2)[t/\tau - \ln(\sqrt{\pi(4Dt + 2\sigma^2)}A/\nu)].} \quad (11)$$

Continuing with our assumption that we are dealing with a small initial population, i.e. the Gauss-asymptotic condition $4Dt \gg 2\sigma^2$ is met before the population becomes large enough that the initial linearization is invalid, $\text{Max}[N(x, t)] \ll N_s$. The maximum population is always at the center,

$$\text{Max}[N(x, t)] = N(0, t) = \nu \frac{\exp(t/\tau)}{\sqrt{\pi(4Dt + 2\sigma^2)}}. \quad (12)$$

In order for the initial perturbation to be small $\nu \ll \sqrt{2\pi}\sigma N_s$, and then providing that these small-perturbation conditions are met, Eq. (11) becomes

$$x_A = \pm 2\sqrt{(D/\tau)t}, \quad (13)$$

so that the wavespeed becomes $v = x_A/t = 2\sqrt{D/\tau}$ when $t \gg \tau$, which is independent of time and A provided the perturbation is small and the linear approximation remains valid. We can show that this result is independent of the shape of $f(x)$, provided it is small and smooth, by taking the inverse FT of $M(x, t)$ [Eq. (8)]

$$N(x, t) = \int dy \frac{\exp[-(x-y)^2/4Dt]}{\sqrt{4\pi Dt}} f(y) \exp(t/\tau). \quad (14)$$

When $\sqrt{4\pi Dt}$ is greater than the width of $f(x)$, this becomes

$$N(x, t) = e^{t/\tau} \frac{\exp[-x^2/4Dt]}{\sqrt{4\pi Dt}} \int f(y) dy. \quad (15)$$

The exponential dependence on x^2 and t in the numerator dominates the algebraic dependence in the denominator, so again we obtain $x_A = \pm 2\sqrt{D/\tau}t$ and $v = 2\sqrt{D/\tau}$.

Thus when population growth is initiated from a small local disturbance, after a short incubation period two waves of population expansion advance in opposite directions at speed $v = 2\sqrt{D/\tau}$ with a shape independent of the initial fluctuation. The wave is driven forward by migration from the increased population density of hunters behind the wave front, which rises to saturation. The controlling parameters for the wave speed are D , the rate at which new territory can be colonized, and τ , the rate of population growth.

3.2. Emergence of farming

Farming emerged gradually over an extended period in various locales within genetically homogeneous populations of hunters and gatherers. In the simulations

carried out with the ASSC model, it was assumed that the newly emerged farming population, a rising from among the hunters H, had completed this process, saturated that locale, and then propagated outward as population F into neighboring regions occupied solely by H who were potential converts X. In this section, we examine the earlier stages of that emergence in a simplified model to provide a mathematical description of the process and to make a point important to understanding the transition from a moving to a stationary cultural boundary as discussed in Sec. 4. We consider a uniform, one-dimensional terrain saturated with a population of H, time-independent until farming is initiated at time zero by a small local population of farming innovators F. Some hunters convert to farming. As those H who convert to farming are genetically identical with the pioneering farmers, there is no need to distinguish a separate population X, and a two population version of the ASSC model suffices:

$$\frac{\partial n_F}{\partial t} = D \frac{\partial^2 n_F}{\partial x^2} + (1/\tau)n_F(1 - n_F - n_H/r) + \gamma n_F n_H, \quad (16)$$

$$\frac{\partial n_H}{\partial t} = D \frac{\partial^2 n_H}{\partial x^2} + (1/\tau)n_H(1 - n_H - r n_F) - r \gamma n_F n_H. \quad (17)$$

We assume that the terrain is favorable for farming, significantly more efficient for food production than hunting/gathering, and define a new parameter, r , which represents the advantage conferred by farming in terms of the total number of people that the land can support $r = N_s^F/N_s^H \gg 1$. We assume also that $n_F \ll 1$ everywhere and $n_H = 1 - \delta_H$ is everywhere close to 1 with $\delta_H \ll 1$ and vanishing initially, while $n_F = f(x) \ll 1$ initially. Under these assumptions, Eqs. (16) and (17) linearize and simplify to

$$\frac{\partial n_F}{\partial t} = D \frac{\partial^2 n_F}{\partial x^2} + (1/\tau + \gamma)n_F, \quad (18)$$

$$\frac{\partial \delta_H}{\partial t} = D \frac{\partial^2 \delta_H}{\partial x^2} - (1/\tau)\delta_H + r((1/\tau) + \gamma)n_F. \quad (19)$$

Equation (18) is identical to Eq. (6) and can be solved by the same procedure with the result that

$$n_F(x, t) = \exp[(1/\tau + \gamma)t] \int \frac{\exp[-(x - x')^2/4Dt]}{\sqrt{(4\pi Dt)}} f(x') dx'. \quad (20)$$

Inserting this result for $n_F(x, t)$ into Eq. (19) and employing the same procedure to solve it yields for $\delta_H(x, t)$,

$$\delta_H(x, t) = r \left(\frac{(1 + \gamma\tau)}{(2 + \gamma\tau)} [\exp(\tau^{-1} + \gamma)t] - \exp(-t/\tau) \right) n_F(x, t). \quad (21)$$

We see from Eq. (21) that with the large value of r and an additional exponential dependence on time, $\delta_H(x, t)$ can grow out of the linear domain far more quickly than $n_F(x, t)$. Consequently, n_H rapidly becomes small where that has happened,

and the conversion term locally drops out of the equation for the evolution of n_F . We infer from these results and the analysis of Sec. 3.1 that in a terrain much more favorable for farming than for hunting, $r \gg 1$, the following holds:

- The initial advance of farming occurs at a speed of $2\sqrt{[D/\tau + D\gamma]}$, a result previously noted in the mathematical biology literature [26, 27].
- Behind but near the advancing toe of the wave, the H population is rapidly wiped out, both by conversion to farming and by lack of success in the competition for land.
- The evolution of farming becomes governed there by the single population dynamics of Sec. 3.1, and the wave speed slows to $2\sqrt{(D/\tau)}$. When $\gamma \ll (1/\tau)$ this has little effect on the shape of the wave front, behind which the F grows to saturation in the absence of H without further conversion; otherwise, the toe of the wave advances more rapidly than the main body, containing the newly converted as well as the demic flow of already established farmers. The role of the relative land fertility, as expressed through the value of r , in the contrapuntal interplay among conversion, growth, and land competition proves key to understanding the dynamic population patterns in the wave of advance of farming in the full three population case, Sec. 3.3, and the conversion of a moving to a stationary cultural boundary in Sec. 4.

The above discussion concerns the growth of farming once the technology has become significantly more productive than hunting and gathering, i.e. $r \gg 1$, and provides a rationalization of the initial conditions used in the simulations of the spread of agriculture in Europe Asia, and Africa with the ASSC model. However, this two-component model can as well be used to describe the much slower emergence of farming as it first becomes competitive with hunting and gathering, i.e. when r first exceeds 1. Clearly, if $r < 1$, there is no motivation to convert, and γ must be taken as vanishing. As the technology slowly improves and r increases beyond unity, γ presumably increases as well. However, for simplicity we shall ignore this slow increase and assign γ a small value which can be taken a constant over the generation time τ . Note that Eq. (16) contains $1/r$ which was ignored in obtaining Eq. (18) by linearization. Restoring it yields a modified version of Eqs. (20) and (21)

$$n_F(x, t) = \exp[(1 - r^{-1})/\tau + \gamma)t] \int \frac{\exp[-(x - x')^2/4Dt]}{\sqrt{(4\pi Dt)}} f(x') dx', \quad (22)$$

$$\delta_H(x, t) = r \left(\frac{(1 + \gamma\tau)}{(2 - r^{-1} + \gamma\tau)} \exp([1 - r^{-1} + \gamma\tau]t/\tau) - \exp(-t/\tau) \right) n_F(x, t). \quad (23)$$

One sees from Eqs. (22) and (23) that with r near 1 and γ small, n_F and δ_H grow slowly, consistent with a gradual evolution of the farming technology and concomitant increase of r and γ before it spreads rapidly by demic flow on a large scale.

3.3. Wave of advance of farming as a moving cultural boundary

We consider now the full three-population case of farmers F invading a one-dimensional terrain favorable for farming, $r \gg 1$, but initially fully occupied by hunters H genetically distinct from the F, some of whom, X, subsequently convert to farming. We imagine that a small number of F colonizes a local region, with the initial value $f(x) = n_F(x, 0) \ll 1$ below saturation everywhere and that of the converts $n_X(x, 0)$ everywhere zero. The ASSC model, Eq. (5), then linearizes at early times to

$$\frac{\partial n_F}{\partial t} = D \frac{\partial^2 n_F}{\partial x^2} + (1/\tau)n_F, \quad (24)$$

$$\frac{\partial n_X}{\partial t} = D \frac{\partial^2 n_X}{\partial x^2} + ((1/\tau) + \gamma)n_X + \gamma n_F, \quad (25)$$

$$\frac{\partial \delta_H}{\partial t} = D \frac{\partial^2 \delta_H}{\partial x^2} - (1/\tau)\delta_H + r((1/\tau) + \gamma)(n_X + n_F). \quad (26)$$

Here, as before, we assume that $n_H = 1 - \delta_H$. Using the methods of Sec. 3.1 of the Supplementary Information, we obtain the solutions,

$$n_F(x, t) = \exp(t/\tau) \int dx' f(x') \frac{\exp[-(x - x')^2/4Dt]}{\sqrt{4\pi Dt}}, \quad (27)$$

$$n_X(x, t) = (\exp(\gamma t) - 1)n_F(x, t), \quad (28)$$

$$\delta_H(x, t) = r n_F(x, t) \frac{1 + \gamma\tau}{2 + \gamma\tau} (\exp[(2 + \gamma\tau)t/\tau] - 1). \quad (29)$$

These results imply the following.

- The farming colony grows and initiates an outward wave of advance moving at the single-population speed $2\sqrt{(D/\tau)}$, Eq. (27).
- The converts, starting from zero, initially grow more rapidly than the farmers because of the factor $(e^{\gamma t} - 1)$ in Eq. (28) and could overtake and overwhelm the farmers were it not for the fact that this early rapid growth depends on the presence of a nearly saturated population of hunters.
- Because of the large value of r favoring agriculture and the strong exponential factor in Eq. (29), δ_H rapidly increases out of the linear domain, and n_H becomes small, eliminating the conversion process from the dynamics before n_X becomes large enough for the converts to compete with the farmers successfully; n_F remains larger than n_X everywhere.
- Over time, the nonlinear, competitive, assimilation-dynamics in Eqs. (5a) and (5c) suppresses the converts, reducing n_X to zero behind the wave.
- Consequently, behind the wave of advance of the farmers, there is an accompanying pulse of converts, initially growing according to Eq. (28) and then decaying because of the effects of the loss of hunters to convert and of subsequent assimilation.

- A moving cultural boundary results behind which the farming population grows to saturation with a small admixture of the genes of the aboriginal hunters.

The final four conclusions were obtained by combining extrapolations from the linear domain with a qualitative analysis of the full nonlinear equations. Numerical simulations support these results in full detail.

Technology diffusion: Eqs. (28) and (29) imply that for given τ, γ , and λ , there is a critical value of farming advantage $r > 1$ below which converts will dominate and suppress both the farmers and the hunters after the introduction of the new technology. The larger the rate of conversion γ , the larger that critical value of r can be. Thus, provided the productivity of agriculture is not too much greater than that of hunting and providing that the rate of conversion is not too slow, converts can out-compete the invading farmers because of the exponential factor in Eq. (28) and change the process of the advance of agriculture from demic flow to technology diffusion. Broadly, this occurs if the number of hunters adopting the technology is greater than the number of converts being assimilated into farming culture. Technology diffusion is illustrated by the simulations displayed in Fig. 2.

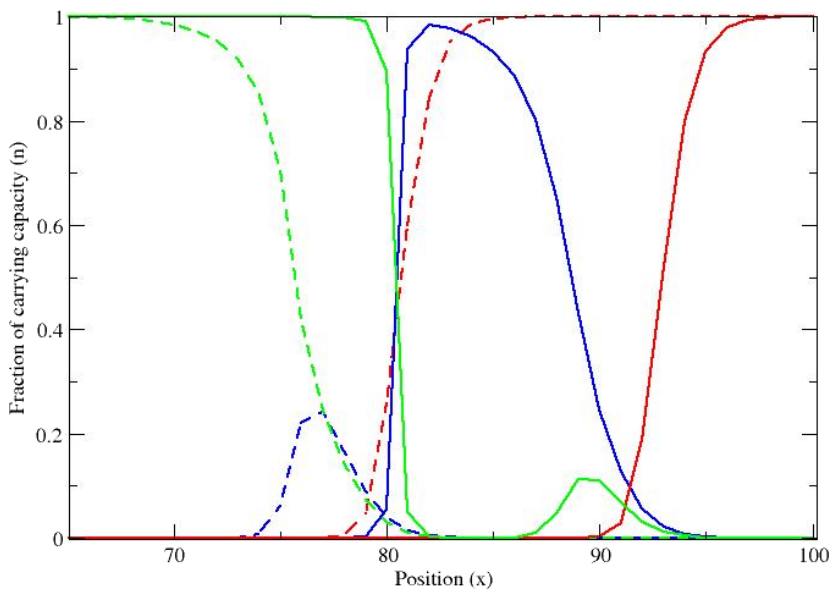


Fig. 2. (Color online) Wavefronts of F (green) H (red) and X (blue) illustrating technology diffusion in homogeneous terrain from a point source of F. At early time (dashed lines) a small group of converts is found in the toe of the wave, but the diffusion is primarily demic. At later times (solid lines) the wave of advance is driven by X (technology diffusion), with a cultural boundary left behind at $x = 80$ the remnant population of F in the toe of the wave ultimately dies out. In this and other figures we use the parameters reported in [1] except where stated otherwise.

4. Steady State Cultural Boundary: Mathematical Analysis

From the ASSC model, there emerges the idea of a cultural boundary at which the population switches to converts retaining their culture from primarily migrants with the culture in which technology originated. The easiest example corresponds to a uniform space (constant D , N_s) with $(1, 0, 0)$ as $x \rightarrow -\infty$ and $(0, 0, 1)$ as $x \rightarrow \infty$. Somewhere in between, at steady state, there is a cultural boundary. To make analytic progress we assume that the time scales τ_i are independent of current population density. Subsequently we check this assumption numerically. For the rest of this section, we redefine dimensionless time and space units $x \rightarrow x/\sqrt{D/\lambda}$, $t \rightarrow \lambda t$, and assume that D , λ and τ are constant, independent of \mathbf{n} , position and time.

A cultural boundary between farmers and converts occurs in an asymptotically steady state with $d\mathbf{n}/dt = 0$, $n_H = 0$. Prior to that, unless $n_F + n_X = 1$ everywhere, the logistic growth term is non-zero, and the global population rapidly relaxes towards saturation, as discussed below.

The steady state solution for n_F must satisfy

$$\frac{d^2 n_F}{dx^2} + n_F n_X (n_F - n_X - 1) = 0 \quad (30)$$

with an equivalent symmetrical equation for n_X . Without loss of generality, we define the boundary by assuming that the state at $\mathbf{n}(x = 0, t = 0) = (0.5, 0, 0.5)$. Due to symmetry $n_F(x) = n_X(-x) = 1 - n_X(x) \equiv n$. Also $n_F - n_X = (2n_F - 1)$. Substituting this into (30) we find that both populations must satisfy:

$$\frac{dn}{dt} = \frac{d^2 n}{dx^2} + n(1 - n)(2n - 1) = 0 \quad (31)$$

at all locations x . The first integral of Eq. (31) with respect to n gives

$$\left[\frac{dn}{dx} \right]^2 - n^4 + 2n^3 - n^2 = a, \quad \rightarrow \frac{dn}{dx} = \sqrt{a + n^4 - 2n^3 + n^2}. \quad (32)$$

Now, since at saturation at $x = -\infty$, $n = 1$ and $\frac{dn}{dx} = 0$, the constant of integration $a = 0$, and, surprisingly, Eq. (32) simplifies to

$$\frac{dn}{dx} = n(1 - n). \quad (33)$$

Integrating from the origin ($x = 0, n = 1/2, \frac{dn}{dx} = 1/4$),

$$\int_{\frac{1}{2}}^n \frac{dz}{z(1 - z)} = \int_{\frac{1}{2}}^n dz \left[\frac{1}{z} + \frac{1}{1 - z} \right] = \ln \left[\frac{n}{1 - n} \right] = x \quad (34)$$

follows, whence

$$n_F = [1 + \exp(-x)]^{-1}, \quad (35)$$

giving a boundary with a unit width (i.e. $\sqrt{D/\lambda}$). This is the width of the cultural boundary (see Fig. 3), and the width is significant because it determines the area in which the cultures overlap. For markers which can become permanently mixed,

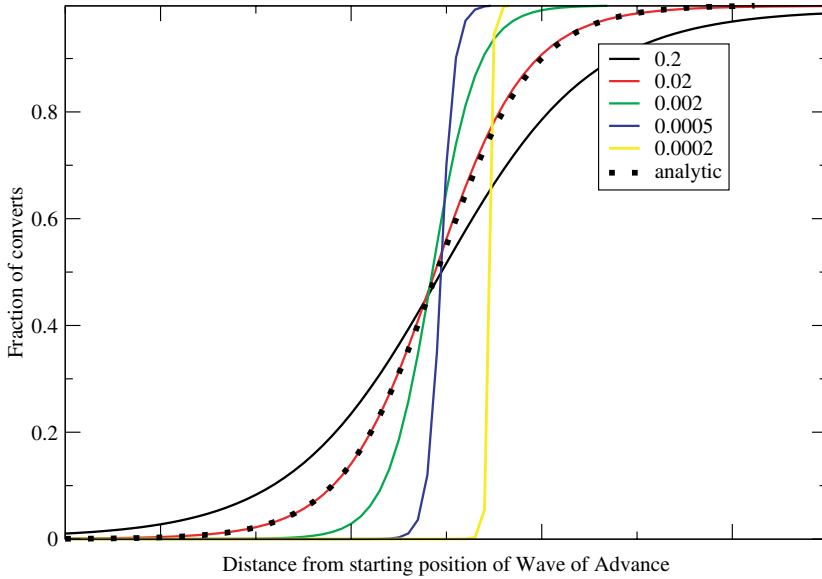


Fig. 3. (Color online) Shape of cultural boundary for the full model [1] in 1D started with $(1, 0, 0)$ at $x = 0$ and $(0, 1, 0)$ elsewhere. with increasing competition λ (values for simulations given in inset, analytic case corresponds to $\lambda = 0.02$); also $D = 1$, $\gamma = 0.0008$ and $\tau = 18.30127$.

such as genes, the size of the overlap will determine the degradation over time of the ability of such markers to measure distinct cultures.

We turn now to the stability of the cultural boundary against fluctuation in one or the other population. Defining $n_{\pm} = n_F \pm n_X$, we find that the total population n_+ obeys the Fisher equation [11] with a weakly density-dependent timescale:

$$\frac{\partial n_+}{\partial t} = D \nabla^2 n_+ + \frac{1}{\tau} n_+ (1 - n_+).$$

Consider a small perturbation δn_+ about the fixed point $n_+ = 1$,

$$\frac{\partial \delta n_+}{\partial t} = D \nabla^2 \delta n_+ + \frac{1}{\tau} \delta n_+ (1 - 2n_+) = D \nabla^2 \delta n_+ - \frac{1}{\tau} \delta n_+.$$

Solving by Fourier transform,

$$\delta n_+ = \int \nu_k e^{ikx} dk \quad \text{with} \quad \nu_k = \frac{1}{2\pi} \int e^{-ikx} dx \delta n_+,$$

gives

$$\frac{\partial \nu_k}{\partial t} = -Dk^2 \nu_k - \frac{1}{\tau} \nu_k, \quad \text{and} \quad \nu_k = \nu_k(0) \exp \left[- \left(Dk^2 + \frac{1}{\tau} \right) t \right].$$

Since D and τ are positive, any perturbation decays away exponentially at a rate greater than $1/\tau$. Turning now to perturbation in the difference n_- ,

$$\frac{\partial n_-}{\partial t} = D\nabla^2 n_- + \frac{1}{\tau}n_-(1 - n_+) + \lambda(n_+ + n_-)(n_+ - n_-)n_-/2. \quad (36)$$

Since we have proved that the stable case relaxes to $n_+ = 1$ on the rapid timescale $\tau \ll 1/\lambda$, this simplifies to

$$\frac{\partial n_-}{\partial t} = D\nabla^2 n_- + \lambda(1 - n_-^2)n_-/2, \quad (37)$$

similar to Eq. (31). Consider the perturbation δn_- to this equation,

$$\frac{\partial \delta n_-}{\partial t} = D\nabla^2 \delta n_- + \lambda(1 - 3n_-^2)\delta n_-/2. \quad (38)$$

To investigate stability, we set some initial perturbation $\Phi(x)$ at $t = 0$,

$$\delta n_- = -\Phi(x) \exp(\omega t). \quad (39)$$

Writing $2n_F - 1$ for the unperturbed n_- for all x , Eq. (38) becomes the Schrödinger equation,

$$-\frac{\partial^2 \Phi}{\partial x^2} + V(X)\Phi = -\omega\Phi, \quad (40)$$

with $V(x) = 1 - 6n_F(1 - n_F)$. Rewriting the solution for n_F from above as $2n_F - 1 = \tanh(x/2)$ gives

$$V(x) = 1 - \frac{3}{2 \cosh^2(x/2)}. \quad (41)$$

An eigenfunction solution is then

$$\Phi = \frac{1}{\cosh^2(x/2)}. \quad (42)$$

As one sees by direct substitution, the corresponding eigenvalue $-\omega$ is zero. As Φ is nodeless, this must be the lowest eigenvalue, so all other ω values are negative and the cultural boundary is stable against all fluctuations except Eq. (42). By differentiating Eq. (35), one sees that this mode consists of a simple time-independent displacement of the position of the boundary. Thus the cultural boundary has *neutral* stability and moves in response to nonuniformity in fertility and thence N_s .

These analytic results come from a linearization of the ASSC equation, which is identical to the linearization of the FKPP equation. In Fig. 3 we show that the analytic result is in good agreement with numerical results for the full, non-linear, ASSC model.

To summarize this section, we have shown that, in the absence of any technological or geographical advantage, a boundary can still form and persist between two cultures; it will be neutrally stable against fluctuations. The boundary region will depend upon D , the diffusion rate of the population, and upon λ , the rate of assimilation of one population by another.

4.1. Geographical effects: pinning

In this section, we show that the cultural boundary can be pinned by a region of low fertility, such as a mountain range, but is destabilised by a region of high fertility.

Let $N_s = N_s^I$ everywhere except between $\pm a$ (region I) while between $\pm a$ (region II) it is $N_s = N_s^{II}$. Define $\tilde{r} = N_s^I/N_s^{II}$ as the ratio of the fertilities, such that $a\tilde{r}$ is a measure of the severity of the infertile region. Finally, recall that the uniform stationary state is $\mathbf{n} = (100)$ or $\mathbf{n} = (001)$.

We assume $n_F + n_X = 1$ through the boundary, with $n_F(-\infty) = 0$; $n_F(\infty) = 1$.

From Eqs. (31)–(33), the assumed stationary solution for $n = n_F$ satisfies

$$\frac{dn}{dx} = \sqrt{A + n^2(1-n)^2}. \quad (43)$$

Since $\frac{dn}{dx}(\pm\infty) = 0$, $n(\infty) = 1$, and $n(-\infty) = 0$, the integration constant A must vanish. Integrating Eq. (43) in region I, we find

$$\int_{n(a)}^{n(x)} \frac{dn}{n(1-n)} = \ln \frac{n}{1-n} \frac{1-n(a)}{n(a)} = \int_a^x dx = x - a, \quad (44)$$

$$n = \frac{\frac{n(a)}{1-n(a)}e^{x-a}}{1 + \frac{n(a)}{1-n(a)}e^{x-a}} = \frac{1}{1 + \frac{1-n(a)}{n(a)}e^{a-x}}. \quad (45)$$

In region II, supposed narrow with $a \ll 1$, we can make the linear expansion $n = 0.5 + gx$ since $n(0) = 0.5$ by symmetry.

One boundary condition at $x = a$ is that the number of people leaving region I is equal to the number arriving in region II, and vice versa, so via Fick's law of diffusion,

$$DN_s^I \frac{dn_I(a)}{dx} = DN_s^{II} \frac{dn_{II}(a)}{dx}.$$

Consequently, $g = (N_s^I/N_s^{II}) \frac{dn_I}{dx}(a) = \tilde{r}n(a)[1 - n(a)] \approx \tilde{r}/4$.

The second boundary condition is $n_I(a) = n_{II}(a)$, i.e. the fractional population density must be the same on each side of the boundary:

$$n(a) = \frac{1}{2} + ga = \frac{1}{2} + \tilde{r}n(a)(1 - n(a))a = \frac{1}{2} + \frac{1}{4}\tilde{r}a,$$

so, in the linear domain

$$\text{for } |x| < a : n(x) = \frac{1}{2} + gx = \frac{1}{2} + \frac{1}{4}\tilde{r}x$$

$$\begin{aligned} \text{for } |x| > a : n(x) &= \frac{\frac{1}{2} + \frac{1}{4}\tilde{r}a}{(\frac{1}{2} + \frac{1}{4}\tilde{r}a) + (\frac{1}{2} - \frac{1}{4}\tilde{r}a)e^{-(x-a)}} \\ &= \frac{1}{1 + e^{-(x-a)}} + \frac{\tilde{r}a/2}{1 + e^{-(x-a)}} \left[1 - \tanh\left(\frac{x-a}{2}\right) \right]. \end{aligned} \quad (46)$$

To check the stability of this boundary, we consider how a small fluctuation in population evolves in time: $n \rightarrow n(x) + \delta n$, where $n(x)$ denotes the stationary

solution. Using Eq. (31) with the time-dependence restored and using the fact that $n = n(x)$ is stationary to eliminate the leading terms, we find to first-order in δn that

$$\frac{d(n + \delta n)}{dt} = \frac{d^2(n + \delta n)}{dx^2} + (n + \delta n)(1 - n - \delta n)(2n - 2\delta n - 1), \quad (47)$$

$$\frac{d\delta n}{dt} = \frac{d^2}{dx^2}\delta n + [6(n - n^2) - 1]\delta n. \quad (48)$$

This can be solved using the Fourier transform $\delta n = \nu e^{\omega t}$ to determine whether δn will grow or decay.

$$\nu'' + [6n(1 - n) - 1]\nu = \omega\nu, \quad (49)$$

where $n = n(x)$ is the steady state solution. Because a is small, we assume that the population distribution will be similar to that of the boundary in infinite terrain, with the barrier causing a small perturbation. The steady state for the population which predominantly occupies the region of negative x , (i.e. $n(x)$) can be expanded everywhere about its unperturbed (i.e. $a = 0$) value n_0 . To first-order in a , then,

$$\begin{aligned} n &= n_0 + \Delta n, \\ n_0 &= \frac{1}{1 + e^{-x}}, \\ \Delta n &= \frac{(1 - e^a)}{(e^x + e^a)(1 + e^{-x})} + \tilde{r}ae^{-(x-a)}[1 + e^{-(x-a)}]^{-2}, \quad |x| > a, \\ &= \frac{1}{2} + \frac{(\tilde{r} - 1)}{4}x, \quad |x| < a. \end{aligned}$$

Because of the symmetry of the problem, Δn must be an odd function of x . Furthermore, it must be positive for $x > 0$ when $r > 1$ (small region of lower fertility) but negative for $x > 0$ when $r < 1$ (small region of higher fertility). Inserting this expansion of n into Eq. (31) yields

$$\nu'' + [6n_0(1 - n_0) - 1]\nu + 6(1 - 2n_0)\Delta n\nu = \omega\nu.$$

Note that this equation is an eigenvalue problem and has the form of Eq. (40) with the small term in δn perturbing the remainder of the lhs, suggesting the expansion $\nu = \nu_0 + \Delta\nu$, $\omega = \omega_0 + \Delta\omega$.

From Eq. (42), we know that the solution with $a = 0$ is

$$\nu_0 = \frac{1}{\cosh^2(x/2)}, \quad \text{and} \quad \omega_0 = 0,$$

and by first-order perturbation theory, with $6(1 - 2n_0)\delta n$ as the perturbation,

$$\Delta\omega = \frac{\int (n_0^2 6(1 - 2n_0)\delta n dx)}{\int n_0^2 dx}.$$

The function $(1 - 2n_0)\delta n$ is everywhere negative for $\tilde{r} > 1$ and everywhere positive for $\tilde{r} < 1$.

Thus the boundary is stabilized by a local decrease in fertility ($\tilde{r} > 1$) at $x = 0$ and destabilized by an increase ($\tilde{r} < 1$).

This is a crucial result, since it shows that within our model we can expect cultural boundaries to be coincident with natural geographical features of low fertility, which is obviously true for many national borders and has broad significance for patterns of human migration.

4.2. Semi-infinite terrain

In the previous section, we assumed that the fertile terrain extends forever in all directions. We now assume fertility goes to zero at $x = 0$, a coastline, and continues at some constant value inland. We show that an FX cultural boundary is unstable in this case, with the landward population advancing.

According to the boundary condition at the interface at $x = 0$, the population density must be equal across the boundary, with nobody in the infertile regions $N(x < 0) = 0$. Since $N = N_s n$ and $N_s = 0$, this does not require a zero-scaled density n at the boundary. However, people will not diffuse into the sea, so the demic flow must be zero, implying $\frac{dn}{dx}|_{x=0+} = 0$.

We now assume that a stationary solution for $n(x)$ exists which describes a cultural boundary. From Eq. 43 above, we know the form for dn/dx ,

$$\frac{dn}{dx} = \sqrt{A + n^2(1 - n)^2}. \quad (50)$$

A cultural boundary at x_0 implies that $\frac{dn}{dx}(\infty) = 0$ and $n(\infty) = 1$. It follows that $A = 0$ and $n(x) = [1 + e^{-(x-x_0)}]^{-1}$.

With this result for $n(x)$, we find

$$\left. \frac{dn}{dx} \right|_{x=0+} = \frac{1}{4 \cosh^2((x - x_0)/2)} \neq 0.$$

Thus the two boundary conditions cannot be satisfied simultaneously under the assumption of the presence of a stationary cultural boundary. The cultural boundary is unstable, it moves towards $x = 0$, generating a solution with F everywhere ($n = 1$).

Simulation of this with the full model (Fig. 4) illustrates the analytic results described above in eliminating a minority coastal culture. There are two competing effects: for high conversion factor, the interface is so narrow that there is no discernable conversion. Furthermore, since the inland population are assimilated before they reach the coast, the situation is effectively the same as in infinite terrain. As the conversion *factor* reduces, so there is more interdiffusion, more contact, and the conversion *rate* increases. For very small conversion factor, the rate reduces again. The green line for $\lambda = 0$ overlies the large λ limit: in both cases the minority culture survives, but the distribution is completely different. In the “tolerant”

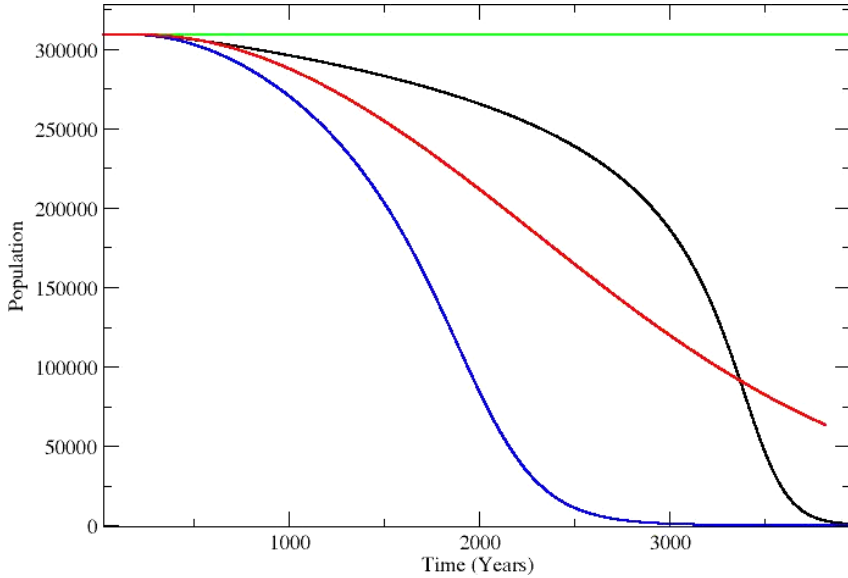


Fig. 4. (Color online) Demise of minority population in a semi-infinite region for various values of λ : Green = 0.005 (sharp boundary in space), Black = 0.001, Blue = 0.0005, Red = 0.0001, Green = 0.0 (no boundary).

$\lambda = 0$ case, the populations mix and the cultural boundary is destroyed, while in the “hostile” large λ case the minority culture stays in its own enclave. Except for these two extremes which allow the minority culture to survive, the coastal population is gradually eliminated. Thus a state of limited tolerance is the most effective way to eliminate a minority culture.

4.3. Large finite terrain

In Sec. 4.1, we proved that a cultural boundary could exist in an infinite region. We now consider a finite region, an island say, and ask whether it can support two cultures.

Assuming that the terrain is homogeneous in N_S for x from $-L$ to L , can the boundary survive? We show that a solution exists for the boundary at $x = 0$, but that this boundary is unstable with respect to small displacements.

We start again with Eq. (43),

$$\frac{dn}{dx} = \sqrt{A + n^2(1 - n)^2}.$$

If we assume impermeable boundaries so that $\frac{dn}{dx}(\pm L) = 0$, then the constant of integration is $A = -n(\pm L)^2(1 - n(\pm L))^2$ which implies either a uniform solution, $n(-L) = n(L)$, or a cultural boundary, $n(-L) = 1 - n(L)$. Assuming the existence of a stable cultural boundary, the symmetry of the boundary condition on dn/dx ,

and the antisymmetry about $n = \frac{1}{2}$ of the boundary condition on n itself, imply that the cultural boundary is at $x = 0$ where $n = \frac{1}{2}$.

Using $n(0) = 1/2$ and integrating Eq. (43) gives

$$x = \int_{1/2}^{n(x)} \frac{dy}{\sqrt{A + y^2(1-y)^2}}. \quad (51)$$

Following the analysis of Sec. 4.1 for stability against small perturbations δn , we start from

$$\frac{d\delta n}{dt} = \frac{d^2}{dx^2} \delta n + [6(n - n^2) - 1] \delta n.$$

Fourier transforming again produces the eigenvalue equation,

$$\frac{d^2 \nu}{dx^2} + [6(n - n^2) - 1] \nu = \omega \nu.$$

We already know the solution for the infinite case, Eq. (35), and its neutrally stable eigenfunction,

$$n_\infty = [1 + \exp(-x)]^{-1}; \quad \nu_\infty = \cosh^{-2}(x/2); \quad \omega_\infty = 0.$$

For large L , we assume the solution is a small perturbation to this

$$n = n_\infty + \Delta n; \quad \nu = \nu_\infty + \Delta \nu; \quad \omega = \omega_\infty + \Delta \omega = \Delta \omega.$$

The eigenvalue equation becomes, to first-order,

$$\frac{d^2 \nu}{dx^2} + [6n_\infty(1 - n_\infty) - 1] \nu + [6(1 - 2n_\infty)\Delta n] \nu = \omega \nu.$$

The perturbing operator in the eigenequation is $[6(1 - 2n_\infty)\Delta n]$, from which the perturbation for ω is given by

$$\omega = \Delta \omega = \frac{\int \nu_\infty^2 6(1 - 2n_\infty)(n - n_\infty) dx}{\int \nu_\infty^2 dx}. \quad (52)$$

To determine whether the boundary is stable, we are interested in the sign of $\Delta \omega$. ν_∞^2 is obviously positive. By comparing Eq. (43) for $n(x)$ for $x > 0$ with the corresponding equation with $A = 0$ for $n_\infty(x)$, and making the analogous comparison for $x < 0$, we find that for

$$x < 0, \quad \frac{1}{2} > n > n_{-\infty}; \quad \text{while for } x > 0, \quad \frac{1}{2} < n < n_\infty.$$

It follows that $(n - n_\infty)$ and $(1 - 2n_\infty)$ have the same sign so that the integrand is positive, as is ω . Thus the perturbation grows exponentially in time, and the cultural boundary is unstable in finite terrain with respect to movement into the minority population.

4.4. Small finite terrain

For large finite terrain, we found a solution as a small perturbation around the infinite system. If the terrain is narrower (i.e. of order the width of the wavefront, $\sqrt{D/\lambda}$), then the perturbation approach may not apply. Starting again with Eq. (51) with

$$A = -n(L)^2(1 - n(L))^2,$$

we can complete the square and rewrite Eq. (51) as

$$x = \int_{\frac{1}{2}}^n \frac{dy}{\sqrt{[y(1-y) + \sqrt{A}][y(1-y) - \sqrt{A}]}}.$$

At a critical width, the difference in populations even at the edges of the terrain may not be large, and the divergent term dominates the integrand, so that we can approximate y in the first term by $n(L)$,

$$x \approx \frac{1}{\sqrt{2n(L)(1 - n(L))}} \int_{\frac{1}{2}}^n \frac{dy}{\sqrt{y(1-y) - \sqrt{A}}}.$$

After some algebra, we find

$$n(x) = \frac{1}{2} + \left[n(L) - \frac{1}{2} \right] \sin \sqrt{2} A^{-\frac{1}{4}} x,$$

which at $x = L$ gives,

$$1 = \sin \sqrt{2} A^{-\frac{1}{4}} L,$$

from which we find,

$$n(L) = \frac{1}{2} + \sqrt{\frac{1}{4} - \frac{\pi^2}{8L^2}}.$$

As $n(L)$ must be real, the above result implies that a stationary cultural boundary cannot exist when $L < \pi\sqrt{D/2\lambda}$ (after reintroducing the units). This corresponds to a small terrain where individuals can retain their culture while diffusing throughout the entire populated area. For larger regions where $L > \pi\sqrt{D/2\lambda}$, there is a wave-like solution, but it is unstable with respect to the motion of the wave. For the parameters used in ASSC, the limit of terrain size within which a boundary can exist (let alone persist) is about 100 km. Thus on medium-sized islands, it is impossible to have two separate cultures, unless movement is severely curtailed (e.g. by mountains or national borders) or assimilation is very fast.

4.5. Stationary cultural boundary in the full model

Our solutions are based on a linearization of the ASSC model, and it is instructive to check with numerical methods whether they are valid for the full nonlinear model. Using code developed in Ref. 1 for the full model, the simulations of a stationary

cultural boundary were done for a variety of strengths of D/λ on a homogeneous background ($N_s = 1$), including the density dependence of τ . The full model has a weak n dependence on the time τ , and the position of the boundary depends weakly on λ . Of course, one cannot simulate an infinite domain, so one was used which was large relative to the boundary width. The proper vanishing-current boundary conditions used in Sec. 4.3 were replaced by fixing n at 0 and 1 at opposite ends and increasing system size until the results were unaffected. This stabilized the cultural boundary at the cost of exponentially-small population flows at the ends. As can be seen in Fig. 3, the analytic results for an infinite terrain and the numerical results are in excellent agreement. This shows that the assumptions of linearization and an n and N_s -independent τ which were required to make analytical progress are reasonable.

4.6. *Transition from moving to stationary cultural boundary*

In our simulation of the advance of farming into Europe, Fig. 1, we observed the formation of a stable cultural boundary running across the interior of the continent from southwest to northeast. The analysis done thus far allows us to identify two interacting effects which can underlie such transitions. One is a local reduction of fertility for farming relative to hunting which reduces r (and possibly γ and λ) and increases τ_F . The other is a local reduction in ease of human movement through the terrain, e.g. through a mountain range where D is reduced as well as fertility. We have already pointed out in Sec. 3.3 that a global reduction of r leads to a transition from demic flow of agriculture to technology flow. A local fertility reduction of sufficient amplitude and width does the same as long as the time for the incoming wave to traverse the region of reduced fertility is long enough for the converts to initiate their more rapid growth. Similarly, a reduction in D conjoined with an increase in τ_F reduces the wave speed of the advancing F, $v = 2\sqrt{D/\tau_F}$, thus allowing the rapid initial kinetics of the growth of X to take over. We illustrate this effect in Fig. 5 with a simulation based on the full ASSC model which shows how a reduction of N_S caused by a mountain in an otherwise homogeneous one-dimensional terrain initiates the formation of a stable, stationary cultural boundary just past the mountain. The early time shows the advance of F and the retreat of H, around $t = 400n_X$, reaches 0.5 for the first time at both a wave of advance and a cultural boundary. Soon after, the X population takes on the technology. We have a boundary of two cultures with equivalent technology which moves back until pinned by the mountain range.

4.7. *Locally advantageous culture; cultural refugia*

Finally, we mention an important stabilizing feature of a cultural boundary, that of a locally advantageous culture. For example, a culture built around growing a particular crop or hunting a certain animal will be unable to spread into regions where that resource does not exist. Thus in addition to the weak geographic effect

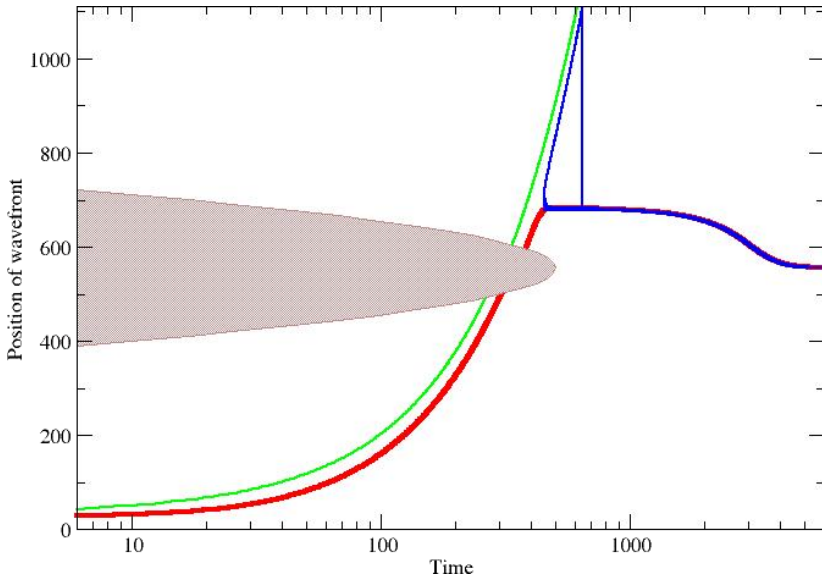


Fig. 5. (Color online) ASSC model in terrain with a substantial hill (Brown shape at left indicates position of hill with reduced fertility (as defined with the σ parameter [1]) going from 17.5 at the bottom to 5.0 at the top. Lines show positions where populations have $n = 0.5$, a surrogate for the position of the wavefront. Green is the wave of retreat of the H. Red is the wave of advance of the F. Blue are the wavefronts of the X. the wave velocity is constant, but we use a log time scale to show the fast wave of advance and the slow-moving cultural boundary.

of pinning a cultural boundary, other human cultural boundaries can be entirely due to biogeographical effects. This can be incorporated into the ASSC model with the land fertility (N_s) having different spatial variation for different populations. For example, in previous work with farming in southern Africa [1], an H-culture without the mediterranean-adapted crops had $N_s^H = 0$ south of a certain latitude, and $N_s^H = N_s^F = N_s^X$ north of it. Another example is the coexistence of hunting/gathering cultures with neighboring farming cultures in cultural refugia within woodlands or jungles unsuitable for the latter. One speculates that the Basque country might have been such a cultural refugium causing its apparent bypassing by the wave of advance of neolithic farming.

5. Demic Movement

5.1. Random movement

5.1.1. The Brownian motion analogy

The demic flow term in the FKPP equation is modeled after the corresponding term in the diffusion equation, thus drawing in the AC model an analogy between the movement of humans and the random displacements of particles undergoing

Brownian motion. In this analogy, the probability distribution $p(\mathbf{r}, t)$ of the displacement \mathbf{r} of a person through an area over a time t as a consequence of such random movement is

$$p(\mathbf{r}, t) = \frac{\exp(-r^2/4Dt)}{4\pi Dt}. \quad (53)$$

The diffusion constant D is one fourth the mean-square displacement per unit time. The latter grows linearly with time and is short-ranged at small times.

5.1.2. Long-range movement

Recently, Brown *et al.* [6] considered the possibility that the random component of early human motion was not Brownian motion (narrowly distributed random distance in a random direction) but a Levy flight (broadly distributed random distance in a random direction). This follows previous suggestions that Levy flights are optimal foraging methods for ants, bees, deer, albatrosses and even ballistic particles [2, 6, 10, 23, 29]. The difficulty with Levy flights is their divergent mean-square random displacement, and Edwards *et al.* [10] have disputed the fit of Levy statistics to the data [10].

The equivalent to the Fisher equation for Levy flights involves fractional derivatives

$$\frac{\partial n}{\partial t} = D_\alpha \frac{\partial^\alpha n}{\partial |x|^\alpha} + \frac{1}{\tau} n(1 - n), \quad (54)$$

where α lies between 0 and 2.

The characteristic function for Brownian motion in one dimension is the Fourier transform of the one-dimensional version $p(x, t)$ of $p(\mathbf{r}, t)$ in Eq. (53),

$$g(k, t) = \exp(-Dk^2t),$$

whereas for Eq. (54) it is $g_\alpha(k, t) = \exp(-D_\alpha|k|^\alpha t)$.

The singularity in $g_\alpha(k, t)$ at $k = 0$ forces the asymptotic behavior to be

$$p_\alpha(x, t) \sim |x|^{-1-\alpha}, \quad (55)$$

so that the second moment of all Levy flights diverges. This long-tail behavior of the distribution of Levy flights is inconsistent with plausible human behavior: one cannot travel an infinite mean-square distance over a lifetime! The observations which led to suggestions of Levy flights are for much shorter movements, so the challenge is to retain this behavior for short-range motion while preserving a finite mean-square displacement. A solution has been advanced by Sokolov *et al.* [28]. They replace the diffusion equation for the probability distribution by

$$\frac{\partial p}{\partial t} - C \frac{\partial}{\partial t} \frac{\partial^{2-\alpha} p}{\partial |x|^{2-\alpha}} = D \frac{\partial^2 p}{\partial x^2}. \quad (56)$$

The Fourier transform of a noninteger derivative with respect to $|x|$ is,

$$F.T. \left(\frac{\partial^{2-\alpha} P}{\partial |x|^{2-\alpha}} \right) = -|k|^{2-\alpha} g, \quad (57)$$

which leads directly to

$$g(k, t) = \exp \left(\frac{-Dk^2 t}{1 + C|k|^{2-\alpha}} \right). \quad (58)$$

For large $|k| \gg k_0 = C^{\frac{1}{2-\alpha}}$, $g(k, t)$ takes the Levy form so that the central region of p for $x \ll 1/k_0$ takes on the Levy form as well. However, for small k , the lowest order singular term at $k = 0$ is $DC|k|^{4-\alpha}$ so that the asymptotic form of p is proportional to

$$p \sim \frac{\alpha DCt}{|x|^{5-\alpha}}, \quad (59)$$

i.e. power law tails with an exponent $5 - \alpha$. For this distribution, the mean square displacement is

$$\overline{x^2} = - \left. \frac{d^2 q}{dk^2} \right|_{k=0} = 2Dt, \quad (60)$$

just as for ordinary Brownian motion. So it seems that Eq. (56) may be a better mathematical description of human movement than Levy flights when including the long-range displacements which can give rise to so-called “leap-frog” effects.

5.2. Demic flow from random movement

The flow term in the FKPP equation is the divergence of a diffusion current density j_D . In terms of the population density N , it is

$$\frac{\partial N}{\partial t} = -\nabla \cdot (-D\nabla n) = -\nabla \cdot j_D. \quad (61)$$

This net current arises from the random movements of many individuals in the population, with more people moving from a denser region to a less-dense one than the reverse. Equation (56) can be rewritten to show a closer resemblance to the diffusion equation.

$$\frac{\partial N(x, t)}{\partial t} = \frac{\partial}{\partial x} \left[D \int dx' K(x, x') \frac{\partial N(x', t)}{\partial x'} \right], \quad (62)$$

with

$$K(x, x') = \frac{1}{2\pi} \int dk [1 + C|k|^{2-\alpha}] e^{ik(x-x')}.$$

In Eq. (62), the flow term on the rhs also takes the form of a divergence of a current j_D which has a linear relation relation to the density gradient but is now non-local,

$$j_D(x, t) = -D \int dx' K(x, x') \frac{\partial N(x', t)}{\partial x'}. \quad (63)$$

Again random movements within the populace give rise to a diffusion current, but now contributions to the current density at x can arise from distant points x' as $K(x, x')$ is asymptotically proportional to $|x - x'|^{-(3-\alpha)}$.

5.3. Purposeful movement

5.3.1. Demic self-diffusion versus purposeful flow

Nevertheless, as already considered by Cohen [8], treating humans as random walkers ignores their purposeful behavior. j_D can be interpreted, in part, as a purposeful response to population pressure. This suggests separating out two contributions to j_D , a purposeful one j_P in response to some pressure, and a random one j_R . We write...

$$j_D = j_P + j_R; \quad D = D_P + D_R, \quad (64)$$

$$j_P = -D_P \nabla N; \quad j_R = -D_R \nabla N. \quad (65)$$

Thus while net flow j_D may vanish at saturation, random motion continues at a level measured by D_R : people continue to move between equally desirable locations for marriage, trade etc. How to partition D into D_P and D_R depends on the conditions, but it is not unreasonable to assume that rational people will not move in the absence of expected gain, so D_P should be greater than D_R and perhaps much greater. Random relocation within a saturated population density, demic self-diffusion, could wipe out over time the genetic gradients introduced by the formation a cultural boundary. That genetic gradients traceable to the introduction of agriculture into Europe have persisted over the millenia since suggests that D_R is indeed very small.

5.3.2. Movement in the presence of others

The prescriptions for the movement of a subpopulation thus far assumes that it is unaffected by the presence of other subpopulations. An alternative and perhaps more plausible assumption is that people will migrate more slowly into occupied land than into unoccupied. The limiting case here is when people migrate only into areas offering better food-growing opportunities, which can be expressed mathematically as a current:

$$J_i = -N_s^i D_i \nabla \left(\sum_j n_{ij} \right). \quad (66)$$

The attractiveness of the new region is now diminished by anyone already there, but the reductive effect of the hunters is limited to the amount of land they can defend, not the land they occupy. This form of the current still gives a migration of farmers into hunting grounds, but not between farming populations. The associated diffusion term is then

$$\partial n_i / \partial t = -(1/N_s^i) \nabla J = (1/N_s^i) \nabla \left[D \cdot N_s^i \nabla \left(\sum_j n_{ij} \right) \right], \quad (67)$$

i.e. incomers consider how difficult it is to access the region (D), how fertile the land is for them (N_s^i) and the total number of people present, rather than solely the incremental amount of food they could grow. Interestingly, this model gives a completely sharp cultural boundary, since flow and hence the boundary width go to zero when the population on either side is saturated. This flow model implies no gene exchange across the boundary.

The above discussion of the purposeful versus random motion implies that in Sec. 4, D should be replaced by D_R , which may be significantly smaller. In practice, when we are considering the wave of advance of farming, the relevant diffusion constant will be $D_P + D_R$. However, when we are considering the FX cultural boundary, only the smaller D_R will apply. This will have the effect of making the cultural boundary much sharper and its motion where unstable much slower.

Insert the value of $D = 7 \text{ km}^2/\text{yr}$ from Ammermann and Cavalli Sforza into Eq. (53). Taking $t = 6000 \text{ yr}$, this would imply a present variance of position of around 400 km. Thus even with this high value of D , we can expect that the genetic signal of an ancient cultural boundary will still be present. This conclusion still holds when we introduce for j_P the more sophisticated flow model of Eq. (66) while retaining for j_R the Brownian motion model. The width of the cultural boundary across which the gene flow occurs is then D_R/λ .

6. Assimilation and Conquest

The λ term describes people of one culture becoming members of another. In the ASSC formulation, people lose their previous cultural identity at a rate proportional to the contact opportunities between people of different cultures and to the size difference of the populations. In testing Renfrew's model of linguistic boundaries, this is a reasonable assumption: assimilated people are likely to adopt the local language. By contrast, genetic markers may be preserved on assimilation, corresponding to $\lambda = 0$. In this case, the only stable boundary would have infinite width (see Fig. 4). In practice this means that any genetic boundary in space is only temporary and vanishes over time.

We note that it would be possible to have a fixed genetic boundary if people of mixed genetic background were less successful in reproduction, the width of such a boundary depending on details of the advantage.

It is also possible that the cultures are at war, killing one another, in which case the λ term for n in Eqs. (5a) and (5c) would be replaced with $-\lambda n_F n_X H(n_F - n_X)$, where the step-function $H(x < 0) = 0$; $H(x > 0) = x$. We have not analyzed this in detail; however, simulations show a continual flow of people into the boundary region, where the population is depleted by war. This population loss at the cultural boundary simulates the cost of an unresolved struggle for territory, and a more accurate description of the process would require modification of the flow equations to introduce sensitivity to the gradients of other populations. A genetic boundary is also stabilized there, though a further complication arises if only males interact by killing while females are assimilated. This would lead to a distinct genetic boundary of Y chromosome markers, but not in the mitochondrial DNA. Such gender differences in heritage are not unusual [7, 17].

Thus many different hypotheses for cultural boundaries can be investigated by adjusting the forms of the interaction term controlled by λ and of the flow terms to describe the model properly.

7. Discussion and Conclusions

We have analyzed further the cultural boundaries discovered in recent simulations of the Neolithic transition using the ASSC model [1]. With simplifying assumptions, we showed that the cultural boundary is stable, exponential-tailed and confined to a region of width $2\sqrt{D/\lambda}$. Simulations with full population dependence (Fig. 1) have only trivially different properties. Although the model has been discussed in the context of the Neolithic transition to farming, the family of models is much more general, and cultural boundaries are a general feature of a wave of advance.

Perhaps the most significant conclusion is that although the ASSC model is derived from fundamental considerations of food production, the additional complication in $\tau(n)$ does not affect the outcome in any significant way. The FKKP equation, with renormalized parameters, remains a reasonable approximation despite all these embellishments. This is similar to our numerical experiment with time-delayed birth: including this gave measurable consequences equivalent to using a different value of τ .

We have further proved a number of mathematical facts about the cultural boundaries described by ASSC. Below a certain terrain size, no boundary of fixed shape can persist. Above this, a cultural boundary can form, but it is unstable in homogeneous terrain moving slowly to allow the larger population to expand. Even in the case where the minority population occupies the more fertile land, no stable boundary can form, one population or the other gains ascendancy. A stable boundary can only exist *and* persist if pinned by some low-fertility inhomogeneity in the terrain.

Using the Neolithic transition parameters [2, 3, 1], the width of the cultural boundary would be hundreds of kilometres. This would allow for considerable gene transfer even as the cultural differences were lost. By contrast, the more recent

arrival of Mediterranean farming into Southern Africa is associated with modern transportation and a much faster diffusion (large D), such that despite the strong competition between European invaders and African farmers, the eventual boundary spans the continent such that it falls below the threshold for a boundary even to form and the populations overlap. With modern communications, forming cultural boundaries may now be history, but the gene flow process is ongoing.

More generally, we have shown that the entire family of models we have considered, single-population for the spread of mesolithic H, two-population for the emergence of farming, and three-population for the spread of an advantageous technology, farming, into occupied territory provides a flexible simulation tool for the testing of hypotheses about the movement of peoples and technologies during human prehistory and history.

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